ORIENTATION OF THE HORSESHOE CRAB, *LIMULUS POLYPHEMUS*, ON A SANDY BEACH

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ABSTRACT

Adult horseshoe crabs (*Limulus polyphemus*) spawn on sandy intertidal beaches and then return toward the water. Field experiments demonstrated that beach slope was more significant than vision in this orientation behavior. Both blinded and normally sighted crabs showed rapid seaward orientation on beaches with a seaward slope of approximately 6°. Orientation performance was poor on a flat beach, although sighted crabs slightly out-performed blinded crabs. The observed orientation behavior was correlated with the large numbers of horseshoe crabs which failed to return to the water after spawning on sand bars or similar habitats lacking a slope gradient.

INTRODUCTION

Adult horseshoe crabs (*Limulus polyphemus* L.) migrate every spring into Delaware Bay and other Atlantic coast estuaries to spawn on sandy beaches (Shuster, 1982; Shuster and Botton, 1985). These sublittoral animals find, and amplex with, a mate, migrate to the intertidal zone to deposit and fertilize the eggs, and then return to the sea. This implies the existence of spatial orientation mechanisms at each critical stage of the reproductive cycle. Although little is known about the mechanism of long distance migrations from the continental shelf to estuarine spawning grounds (Botton and Ropes, 1987), Rudloe and Herrnkind (1976) showed that submerged crabs near breeding beaches can orient in response to wave surge. Barlow *et al.* (1982) found that visual cues are important during mating, and Barlow *et al.* (1986) suggest that light may be a significant environmental factor associated with seasonal and diurnal variability in mating activity. Visual stimuli may elicit other behavioral responses including direction and speed of locomotion (Cole, 1923; Northrup and Loeb, 1923; Ireland and Barlow, 1978) and telson and gill movements (Powers and Barlow, 1985).

The orientation cues which enable horseshoe crabs to return to the water after mating have not been previously considered. This behavior has important ecological consequences because animals "stranded" on an exposed intertidal beach are subjected to physiologically stressful conditions, including high temperatures, desiccation, and osmotic imbalance (Herrnkind, 1983). Among shore zone arthropods, both visual cues (*e.g.*, sun, moon, polarized light, landmark orientation) and nonvisual cues (such as beach slope) are known (Herrnkind, 1972, 1983; Schöne, 1984). In 1985 during a preliminary beach survey of Delaware Bay in the area of Fortescue, New Jersey, we observed large numbers of live horseshoe crabs burrowed on a relatively flat section of exposed intertidal beach at low tide. We hypothesized that this aberrant

behavior resulted from the inability of the animals to orient seaward in the absence of beach slope; in this report, we present an experimental test of that hypothesis. Orientational behavior of sighted and blinded individuals on sloped and flat beaches were quantified to evaluate the importance of beach slope and light for adult horseshoe crabs.

Materials and Methods

All experiments were conducted between 26 May and 7 June 1986 at the New Jersey Oyster Research Laboratory (NJORL), located on the Delaware Bayshore in Cape May County, New Jersey. The study area was located just north of the laboratory. One site had a slope and sediment composition typical of this relatively uniform and undisturbed beach (Shuster and Botton, 1985). During spring, these beaches have a slope of some 6.4 degrees in approximately a westerly direction. The second site was a flat sand bar formed by the outlet of a salt marsh creek. It was located approximately 100 m north of the sloped beach site, also with the bay toward the west. Horseshoe crabs spawned in large numbers in this and adjacent areas during full moon high tides. Both sites within the study area provided similar visual fields: an open horizon in the seaward direction and a line of vegetation (mainly *Phragmites*) above the high water line in the landward (easterly) direction.

Orientation was studied within "arenas" modeled after Mrosovsky and Shettleworth (1968). On each beach, a 4-m radius circle was inscribed and a 30-cm trench dug along its perimeter. Stranded horseshoe crabs and any large pieces of debris were removed from the arena before use. The arena was divided into 16 equal sectors of 22.5° each. Sector 1, beginning at compass point north, was arbitrarily designated as 0°, sector 2 began 22.5° in a clockwise direction, *et seq.*

Adult male horseshoe crabs were collected from the bay immediately before the study of their behavior. Crabs with missing appendages, or with damaged, missing, or heavily encrusted eyes, were discarded. Those crabs kept out of water for more than 3 minutes were thoroughly wetted down before the trial. The animals used in the blinding experiments were prepared by drying the carapace around the lateral and median eyes using a paper towel, and then placing patches of opaque adhesive duct tape over the eyes.

Each of the four combinations of beach slope and vision, *i.e.,* sloped beach/sighted, sloped beach/blinded, flat beach/sighted and flat beach/blinded, were run on at least two separate days, with a total sample size of not less than 41 individuals per combination (range, 8–23 crabs per run). Crabs were tested individually to avoid behavioral interactions because they often pause or change direction when other crabs are encountered along the beach (pers. obs.). To begin a trial, the top few cm of sand in the arena was smoothed using a wooden board to remove the track of the previous animal; this procedure also disrupted any possible gradients in surface sediment moisture. The crab was placed in the center of the arena facing away from the water and on a line perpendicular to the shoreline. If the animal burrowed in place, it was lifted out of the sand and re-started; if it burrowed twice in succession, it was rejected.

A trial was completed when the animal's prosoma crossed the perimeter of the arena. Animals failing to complete a trial, or which burrowed, or which remained motionless on the surface of the sediment for 5 consecutive minutes were recorded but not used in the statistical analysis of this behavioral data set. Investigators recorded the elapsed time of the test, the section of the arena from which the crab exited, and the number of pauses longer than 30 s. The linear distance of the path was measured by placing a metered string along the animal's track; a sketch of the path for each trial was made.

TABLE I

Comparison of the number of "disoriented" (live, rightside-up) Limulus polyphemus *on flat and sloped beaches in Delaware Bay on each of three days during Spring 1986*

| Date | Mean no. disoriented crabs per 15-m transect | | n | t |
	Flat	Sloped		
23 May	55.2	12.2	5	4.552**
24 May	93.3	9.8	4	3.342*
25 May	101.5	4.5	4	3.623*

n = number of replicate 15-m transects counted on each type of beach, t = t-statistic comparing mean number of crabs on each type of beach. Means on flat beach significantly greater than mean number on sloped beach at $P < .05$ (*) or $P < .005$ (**).

The performance of a group of crabs was assessed using a number of variables including percent crossing the perimeter, time required to leave the arena, linear distance travelled, and the number of pauses and circles made by the animals. We calculated each animal's "meandering score" as the linear distance of the path divided by the radial distance (4.0 m) (Mrosovsky and Kingsmill, 1985). We computed mean vectors, mean angles of orientation, and 95% confidence intervals for each group of animals (Zar, 1984, p. 428). All animals were assumed to cross at the midpoint angle in the appropriate sector. The Rayleigh test (Zar, 1984, p. 443) examined the null hypothesis that there was no mean population direction. Differences between mean angles were analyzed using the Watson-Williams procedure (Zar, 1984, p. 446).

We surveyed the "disoriented" crabs in transects on the flat and sloped beaches on 23–25 May. Disoriented crabs were defined as those live animals remaining rightside-up on the breeding beach at low tide, as distinguished from the normal behavior, which is to follow the receding tide and spend the low tide period on the intertidal sand flat. Live upside-down crabs, "stranded" by wave action, were not counted.

RESULTS

Surveys of disoriented crabs

The number of disoriented (live, rightside-up) stranded crabs was significantly higher on the flat beach than the sloped beach on each of the three days (Table I). Since similar, or perhaps slightly lower numbers of mating horseshoe crabs actually approached the flat beach compared with nearby sloped beaches (based on Botton, 1982 and personal observations during the 1986 field season), the accumulation of disoriented crabs on the flat beach is not likely to be a numerical artifact. Similar dense concentrations of disoriented crabs were observed near creek mouths along Delaware Bay north of our study area during a survey in 1985. In contrast, only about 20–25% of live crabs stranded on sloped beaches during May, 1986 were rightside-up (disoriented) animals; the remainder were stranded upside-down as a result of wave action and/or telson abnormalities (R. E. Loveland and M. L. Botton, unpub. data). Approximately 24–34% of the disoriented individuals on the flat beach were stranded as mated pairs (males amplexed to females). By comparison, only 46 disoriented mated pairs (of a total of 4247 stranded crabs) were found on two sloped 90-m study beaches between 15 May and 21 June 1986 (R. E. Loveland and M. L. Botton, unpub. data).
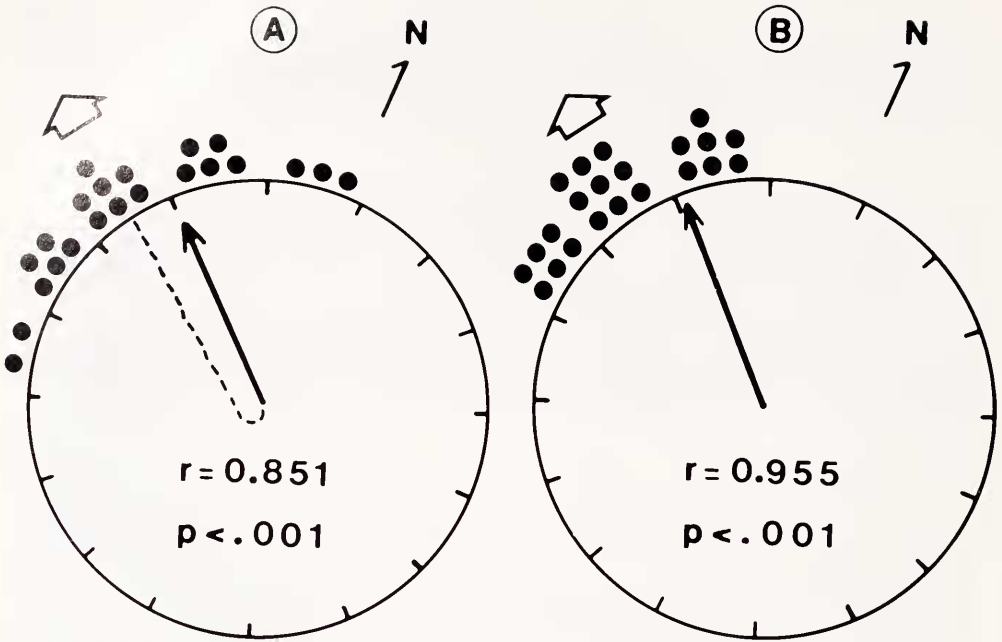
FIGURE 1.   Orientation behavior of horseshoe crabs with normal vision on a sloped beach. Run A held 26 May, 1610–1850, bright sunlight, wind W less than 5 mph. Run B held 2 June, 1057–1323, cloudy with occasional drizzle, wind NNE 15 mph. Length and direction of mean vector r shown by solid arrow; Rayleigh's Test indicated significant mean population direction in both runs. Seaward direction indicated by open arrow. Typical "fish hook" path followed by a crab is shown in A.

Orientation on sloped beach. All sighted crabs showed strong seaward orientation (Fig. 1). The path followed by nearly all crabs in these trials was the "fish hook" pattern illustrated in Figure 1a. Typically, a crab first walked in the direction it was placed (in this case, uphill) before turning to its left or right. More crabs turned left (n = 26) than right (n = 16) but the difference was non-significant ($\chi^2 = 2.38$, .25 < P < .10). There was no significant difference in mean angle between a group of crabs run in late afternoon (n = 23) and a second group (n = 23) run in midday (Watson-Williams test, F = 0.229, n.s.). In both trials, 22 animals (96%) completed the test and there was no significant difference in the time it took to complete the test (Mann-Whitney U-test, z = 0.493, n.s.). The meandering score was significantly lower in the late day group (U = 365.0, P < .005). Pausing and circling behaviors were noted only five times each (Table II).

Blinded crabs also showed strong seaward orientation on the sloped beach (Fig. 2). Mean angles of crabs tested in early morning and mid-afternoon were virtually identical. In both the morning and afternoon experiments, 20 animals (87%) completed each trial. Animals in the morning trial took significantly longer (Mann-Whitney U-test, U = 352.5, P < .001) and had a higher meandering score (U = 316, P < .002) than the afternoon group. This difference was probably related to a steepening of the beach slope before the afternoon trial, which was caused by strong wave action several tidal cycles earlier. Blinded animals followed the typical fish hook path described above; the direction of turning was random (20 to the left, 21 to the right). No blinded animal circled in either trial and pausing was infrequent (Table II).

Orientation on flat beach. Horseshoe crabs with normal vision had difficulty ori-

Measures of orientation performance (means and standard errors = SE) of horseshoe crabs on sloped and flat beaches

	Sloped beach				Flat beach					
	Normal vision		Blinded		Normal vision			Blinded		
Variable	A	B	A	B	A	B	C	A	B	C
Time to completion	88.9	103.3	134.7	58.1	271.9	128.8	192.1	183.2	395.7	374.9
SE	11.8	16.4	19.1	5.6	53.5	37.6	22.0	61.3	137.2	64.8
Meandering score	1.21	1.43	1.48	1.37	2.36	2.15	2.01	1.72	2.04	3.45
SE	0.03	1.13	0.04	0.07	0.49	0.32	0.15	0.27	0.28	0.37
No. of pauses	0.04	0.26	0.22	0.17	0.50	0.50	0.13	0.75	1.87	1.06
SE	0.04	0.12	0.09	0.10	0.20	0.31	0.07	0.41	0.62	0.36
No. of circles	0.09	0.13	0.00	0.00	1.00	0.60	1.17	0.75	0.67	2.33
SE	0.06	0.07	0.00	0.00	0.35	0.31	0.31	0.31	0.21	0.52
Number completing	22	22	20	20	11	8	21	6	6	13
Number burrowing	0	0	1	1	4	1	0	1	4	2
Number stopped without burrowing	1	1	2	2	1	1	2	1	5	3
Total number in run	23	23	23	23	16	10	23	8	15	18

Time to completion (in seconds) and meandering scores based on only those animals crossing the perimeter of the 4-m radius testing arena. Letters at top of column designate individual runs.

enting on the flat beach. Three separate runs were conducted. In afternoon runs under both overcast and sunlight conditions, values of Rayleigh's z indicated that crabs were not significantly oriented in any direction (Fig. 3a, b). In the third run, on a sunlit morning, there was significant orientation in a seaward direction (Fig. 3c). However, four animals which exited through a seaward-facing sector were actually travelling parallel to the shoreline when they crossed the perimeter.

Sighted crabs on the flat beach had a 10-fold increase in pauses and number of circles, and higher meandering scores, compared with animals on the sloped beach (Table II). Nine of the 40 animals (22.5%) tested in the three runs either burrowed or stopped moving for 5 minutes, thus failing to complete the test.

Horseshoe crabs behaved differently on the flat beach than on the sloped beach, although variability was high among those tested. Very few paths formed the fish hook pattern described earlier. Initially, crabs moved rapidly in the direction they were placed, but typically they turned and slowed down within the first meter. Many crabs reared up on their pedipalps and moved slightly from side to side. This behavior was often followed by circling, which in most cases began within 1 m of the release point, although some animals made wider loops, "figure 8's," or both (Fig. 3a).

Blinded crabs were even more disoriented on the flat beach than were the sighted individuals. The percentage of crabs completing the test was the lowest of the four experimental combinations (Table II). Seven of the 41 crabs (17%) burrowed before crossing the perimeter and another 9 (22%) stopped moving without burrowing. Of those crossing the perimeter, the direction was random (Fig. 4). There was no significant difference in the time to complete a trial between the three groups; however, crabs in the third run had a significantly higher meandering score than those in the first two.

In comparing sighted and blinded crabs on the flat beach, the blinded animals took longer ($\bar{x}$ = 333.8 s) than sighted animals ($\bar{x}$ = 201.4 s) to complete the test (U = 663, $P < .05$). The meandering scores were not significantly different between the
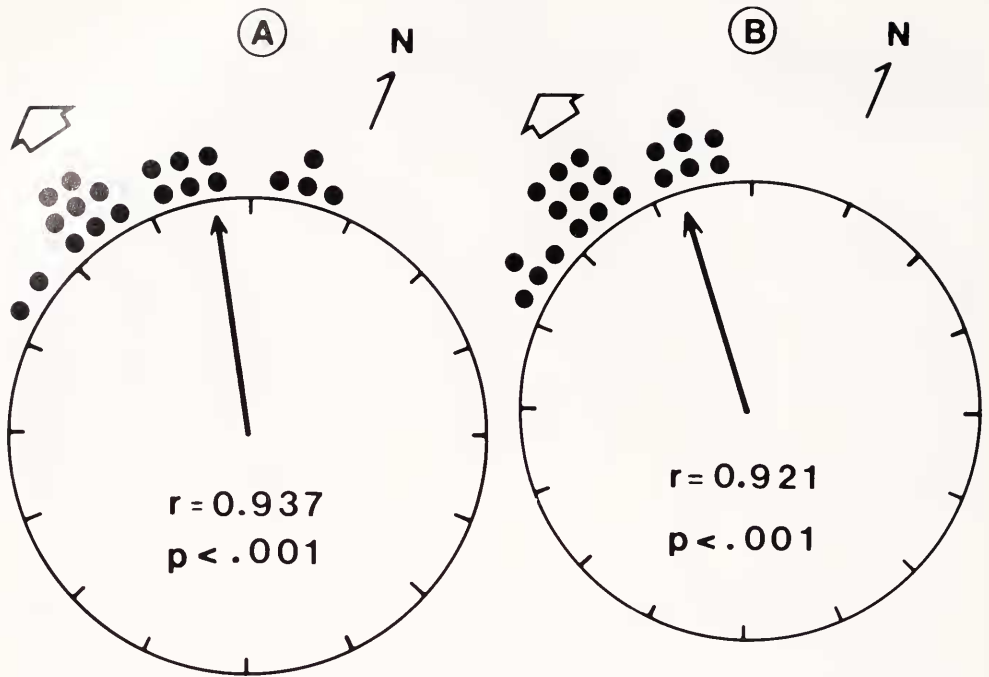
FIGURE 2.   Orientation behavior of blinded horseshoe crabs on a sloped beach. Run A held 28 May, 0710–1038, heavy cloud cover with mist, wind WSW 5 mph. Run B held 4 June, 1250–1600, bright sun, wind S 10 mph; slightly steeper slope than Run A because of strong wave action during previous 48 hours. Length and direction of mean vector r shown by solid arrow; Rayleigh's Test indicated significant mean population direction in both runs.

sighted crabs and the first two groups of blinded crabs, but both were significantly lower than the third group of blinded crabs (Kruskal-Wallis test, H = 11.54, P < .005).

DISCUSSION

As noted by Herrnkind (1983), orientation by shore zone arthropods could potentially involve visual and/or nonvisual guideposts. Among arthropods, visual cues are important in various amphipods, isopods, decapods, insects, and wolf spiders (Herrnkind, 1972). In contrast, beach slope has been demonstrated to be involved in orientation far less frequently (Hamner *et al.,* 1968; Craig, 1973). At our Delaware Bay study area, there appears to be a strong visual contrast between the dark horizon in a landward direction and the open horizon in the bayward direction; therefore, we considered the possibility that horseshoe crabs on sandy beaches might be employing vision.

There is considerable precedent in the literature concerning the behavioral responses of *Limulus* to light. Cole (1923) found that asymmetrically blinded animals 20–60 mm in diameter (which he erroneously considered to be adults) circled most frequently in the direction of the remaining lateral eye. Northrup and Loeb (1923) found that young crabs (*ca.* 15 cm length) were negatively phototropic. *Limulus* can also detect polarized light (Waterman, 1950), but at present there is no experimental evidence implicating this in any known behavioral response. More recently, Barlow and collaborators (*e.g.,* Barlow *et al.,* 1980) have shown the presence of a circadian
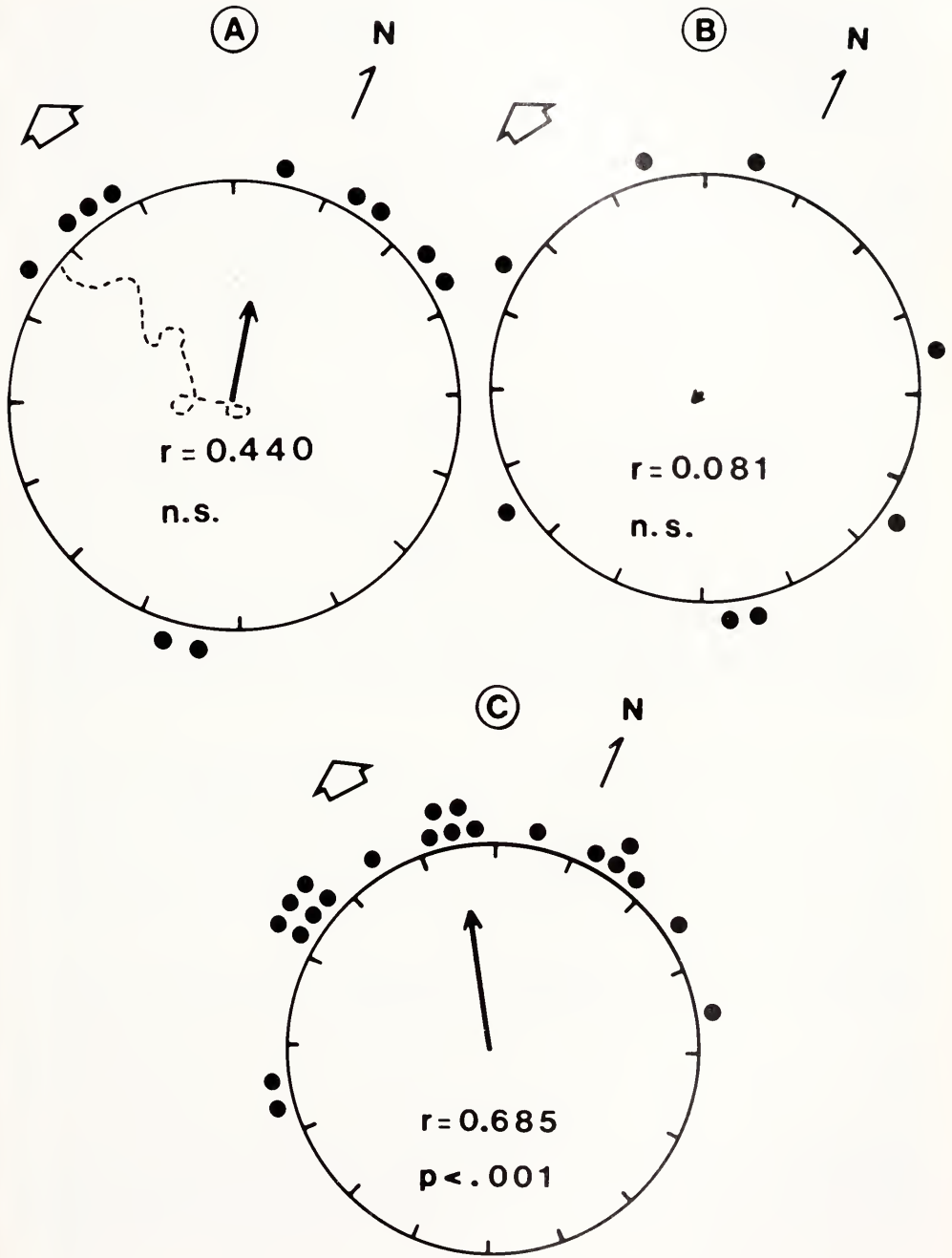
FIGURE 3. Orientation behavior of horseshoe crabs with normal vision on a flat beach. Run A held 27 May, 1555–1930, heavy cloud cover, wind calm. Run B held 28 May, 1622–1747, bright sun, wind WSW 5 mph. Run C held 5 June, 0825–1200, bright sun, wind S 5 mph. Length and direction of mean vector r shown by solid arrow; Rayleigh's Test rejected the null hypothesis of no mean population direction in Run C only. Seaward direction indicated by open arrow. Typical path followed by a crab is shown in A.
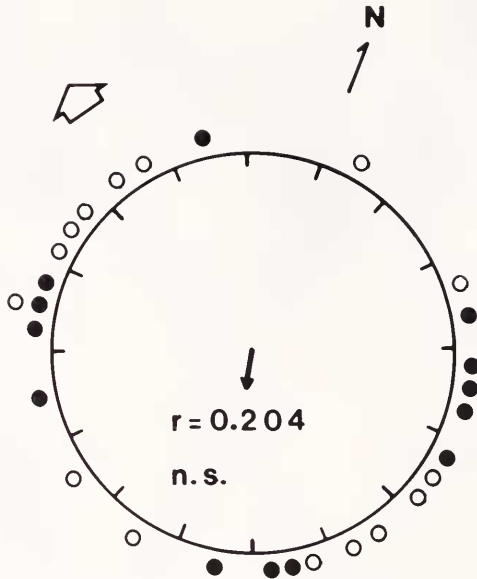
FIGURE 4.   Orientation behavior of blinded horseshoe crabs on a flat beach. Runs A (30 May, 1314–1450, wind W 5 mph) and B (31 May, 0748–1205, wind W 5 mph) were combined (open circles) because of the small number of animals completing each trial. Run C (7 June, 0730–1245, mostly sunny, wind S 5 mph) shown with filled circles; length and direction of mean vector r (solid arrow) based on Run C data. Population showed random orientation. Seaward direction indicated by open arrow.

rhythm in ommatidial morphology and visual sensitivity, modulated by a clock in the animal's brain. Visual sensitivity is higher at night, enabling males to recognize female "models" even during the evening (Barlow *et al.*, 1982). Blinded crabs released in the subtidal environment were more disoriented than sighted crabs (Ireland and Barlow, 1978). However, both blinded and sighted submerged crabs were capable of orienting in the vicinity of the breeding beach when wave surge was present (Rudloe and Herrnkind, 1976).

Experiments with blinded and sighted crabs on both sloped and flat beaches indicate that beach slope, not visual stimuli, is the primary cue used by horseshoe crabs to return to the water. Both blinded and sighted animals showed rapid seaward orientation on a sloped beach. In contrast, orientational performance was severely impaired on a spawning beach lacking slope. Sighted and blinded crabs showed pausing and circling behaviors on the flat beach far more frequently than on the sloped beach. Circling, accompanied frequently by the animal's rearing up on their pedipalps, may have been an attempt to obtain directional information from gravitational cues. Since these directional cues were lacking in the flat arena, it is not surprising that meandering scores on the flat beach were higher, and many animals either burrowed, stopped moving entirely, or left the arena on a heading that took them away from the water.

The physiological basis for the observed response to beach slope is not clear. Despite the extensive use of *Limulus* in neurophysiological research, no statocyst or other balance organ has been described. However, proprioreceptors have been identified from the gnathobases and joints of the walking legs (Barber, 1956, 1960; Pringle, 1956; Barber and Hayes, 1964). We hypothesize that stimulation of these receptors in a crab walking "uphill" may elicit a turning response which then directs crabs down the slope, toward the water. A crab can presumably detect when it has started

"downhill," since once on this heading, turns are infrequent. The information registered by these proprioreceptors would be constant on a flat beach, which may underlie their lack of orientation. It seems unlikely that mechanoreceptors on the dorsal carapace (Kaplan *et al.,* 1976) or lateral spines (Eagles, 1973) are involved in beach orientation, although they may provide positional information under different circumstances.

The comparison between the responses of blinded and sighted animals on the flat beach suggests a possible secondary role for vision in sandy beach orientation. One of three groups of sighted crabs showed significant seaward orientation (Fig. 3), but why this group did, and the other two did not, is not apparent. Overall, sighted crabs on the flat beach exhibited somewhat better orientation (as measured by percent finishing, number of pauses, and meandering scores) than the blinded crabs on the same arena, although their performance was much poorer than the blinded crabs on the sloped beach.

A comparable and ecologically similar orientation problem confronts female sea turtles after egg laying. In these animals, in contrast to *Limulus,* the primary cues are visual. Females, as well as hatchlings, assess the brightness differential between the open, seaward horizon and the darker, vegetation-lined landward horizon (Ehrenfeld and Carr, 1967; Mrosovsky and Carr, 1967; Mrosovsky and Shettleworth, 1968; Mrosovsky, 1970). In comparison, there is some evidence for positive geotropism among hatchlings (Parker, 1922; Van Rhijn, 1979), although Mrosovsky and Kingsmill (1985) point out that on many turtle nesting areas, slope is very irregular and not as good a predictor of seaward direction as is the open horizon. This configuration is markedly different at the Cape May shore of Delaware Bay, where undisturbed beaches consistently have a seaward slope. A positive geotaxis is therefore a reliable orientation behavior for adult horseshoe crabs, whereas for sea turtles, it is not. However, it might be adaptive for a species to have a secondary orientation mechanism should the primary system fail. For sea turtles, geotaxis may function, albeit weakly, when vision is impaired (Van Rhijn, 1979); a similar hierarchy of cues exists in the amphipod, *Orchestoidea corniculata* (Herrnkind, 1983). For horseshoe crabs, vision may be of some limited value when the crabs become stranded on a flat beach, but many animals which spawned on this type of beach are unable to find the water only a few meters away (Table I). Under these circumstances, it seems adaptive for horseshoe crabs to burrow because it conserves energy and keeps their book-gills in contact with cooler, moist sand. If high tide during the next day is of equal or greater amplitude than the one on which they were stranded, the crabs will have a good chance of survival, but if tidal heights are declining, there may be localized, large-scale mortality.

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